

THE STRUCTURE OF MONOTROPSIS AND THE CLASSIFICATION OF THE MONOTROPOIDEAE

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The original observations here to be presented refer exclusively to *Monotropis odorata*, and are based entirely on material furnished by Mr. Willman Spawn, of Washington, D. C., to whom I am most cordially grateful. These observations, in connection with my previous studies (3, 4, 5, 6) have led me to certain conclusions as to the natural arrangement in tribes of the genera of Monotropeoideae. I follow the statement of observations, therefore, with a suggested solution to a problem which has engaged, among other authorities, Gray (11), Drude (9), Andres (1), and Domin (7). The arrangement proposed is, of course, tentative and subject to amendment; it is based on a body of knowledge which could have been extended by further study; but such is the nature of all scientific hypotheses.

For access to some of the literature, I am indebted to the California State Library. The borrowing and lending among libraries, which are so helpful to the student, serve him with so little trouble to himself that he can easily overlook his obligation to the system and to the libraries which participate in it.

Dr. Katherine Esau, of the University of California at Davis, has helped me, as noted below, to understand the phloem.

At this stage in my studies of the Monotropeoideae, I must not fail to acknowledge a considerable debt to Dr. W. L. Jepson, at whose suggestion I first undertook them. Correspondence with Dr. H. Andres, with Dr. W. H. Camp, and with Mr. Willman Spawn has been a constant source of information and of inspiration.

THE NOMENCLATURE AND DISTRIBUTION OF MONOTROPSIS

Monotropis, the third in order of discovery among the genera of Monotropeoideae, includes three species, all confined to the southeastern United States. The nomenclature and geographic distribution, compiled largely from the writings of Small (23, 24, 25) are as follows:

MONOTROPSIS Schweinitz *ex* Elliott Fl. S. Car. and Ga. 1: 478. 1817. *Schweinitzia* Elliott *apud* Elliott l. c. *Cryptophila* Wolf in Amer. Midland Nat. 8: 115. 1922.

1. MONOTROPSIS ODORATA Elliott, *op. cit.*, p. 479. *Schweinitzea* [!] *odorata* Rafinesque in Amer. Monthly Mag. 3: 99. 1818. *Schweinitzia caroliniana* G. Don, Gen. Syst. 3: 867. 1834. *Cryptophila pudica* Wolf, *op. cit.*, p. 117. Maryland to Georgia and Alabama, in and near the mountains; type locality, Stokes County, North Carolina.

2. *MONOTROPSIS REYNOLDSIAE* Heller, Cat. N. Am. Pl. 5. 1898. *Schweinitzia Reynoldsiae* Gray in Proc. Am. Acad. 20: 301. 1885. Florida; type locality, near St. Augustine.

3. *MONOTROPSIS LEHMANIAE* Burnham in Torrey 6: 235. 1906. North Carolina; type locality, Roaring Gap on the Blue Ridge.

In most of the standard accounts of the *Monotropoideae*, the generic name *Schweinitzia* is used. This name originated on the same page as *Monotropsis*, where Elliott included the following remark: "I hope, however, that instead of the compound name by which Mr. Schweinitz has designated this genus, to which Botanical critics will object, the name of *Schweinitzia* may be given to it. . . ." The generic description, nevertheless, is under the heading of *Monotropsis*; the specific epithet "1. *Odorata*" on the next page must be held to be published under *Monotropsis*; no binomial under *Schweinitzia* can be recognized as published by Elliott. *Schweinitzia* was treated as valid in two publications of the following year, respectively by Nuttall (20) and by Rafinesque (22); it was the latter who first made the familiar combination *Schweinitzia odorata*.

The authors just mentioned were nearer in time to Linnaeus than to us, and observed certain usages of Linnaeus which we have abandoned. Linnaeus treated the relative antiquity of names as of little consequence. One of his services to science—his greatest service, in the unappreciative view of Greene (13)—was a purge, a veritable massacre, of such names as *Lilio-Narcissus*, *Cyperoides*, and *Chamaerhododendros*. He made good form a postulate, and seems to have assumed that this feature of his system would be of material influence in keeping it in use. In view of the Linnaean precedent, Elliott and Nuttall, Rafinesque and Gray, felt no compulsion to use any name which seemed to them in poor taste. Some fifty years after the name of *Schweinitzia* came into use, an international botanical congress adopted a code according to which priority takes precedence of usage and good taste; and after some twenty years more, a new purge of names, guided by the newer postulate, was carried through. This was by many felt to be an unprovoked outrage. The objectors, however, found themselves entrapped; only to a limited extent has it been possible to avoid using the names put forward by Otto Kuntze. It was he (19, p. 391) who resurrected *Monotropsis*. We of the present time can find no excuse not to follow him; and to our taste, one name seems hardly worse than the other.

The Reverend W. Wolf (26) studied *Monotropsis odorata*, as it occurs at St. Bernard, Cullman County, in northern Alabama, for some twenty years before he published it as new genus and species, *Cryptophila pudica*. In the early stages of his work, he had recognized the true identity of the plant; it was the writings of Gray (11), which describe the fruit as a five-celled

capsule, that misled him into supposing he had something new. Small (23, 24) had erred as Gray had, but he was not deceived by the revelation of the true characters of the ovary and fruit; he presently (25) reduced Wolf's names. The observations of Wolf were extensive and accurate; in matters of gross morphology, what follows is in part confirmation of his work, and in part stated on his authority.

MATERIAL

The material furnished by Mr. Spawn consists of three flowering shoots of *Monotropsis odorata*, with roots, collected in Maryland in April of 1938; and of a juvenile shoot and a fruit collected late in July of the same year. These objects had been fixed in Bouin's fluid, and came to me preserved in alcohol; I have found them very well prepared.

THE ROOT SYSTEM

The root system is the permanent member of the plant. It shows, on sectioning, scattered scraps of mycorrhiza on the surface; it cannot be said to be generally covered by a heavy layer of mycorrhiza.

The diameter of roots varies from about 0.2 mm. to about 1.0 mm. A longitudinal section of one of the smaller ones (I have been unable to follow any of the larger ones to the tip) shows a very feebly developed cap, formed by periclinal divisions of cells of the dermatogen, which is continuous over the tip within the cap (Pl. 9, fig. 2). The distal end of the plerome appears to be separated from the dermatogen by a single layer of cells belonging to the periblem.

In the mature region, a small root such as this would show two strands of xylem (Pl. 9, fig. 3); larger ones show from three to five strands of xylem (Pl. 9, figs. 4-6). Lignified conducting cells of the xylem are present in the centers of smaller roots; in larger roots, the cells in the center remain undifferentiated and constitute a pith. No cambial activity is recognizable. It has seemed possible to recognize the boundary between pericycle and cortex by a difference in the size of the parenchymatous cells, those of the pericycle being smaller; it has not been possible to recognize an endodermis differentiated by the presence of Casparian strips. Secondary roots and adventitious buds (Pl. 9, figs. 5, 6), the latter in much smaller numbers than the former, originate in the pericycle in the planes of the strands of xylem; each root bears, therefore, a number of rows of these equal to the number of strands of xylem in the stele.

THE SHOOT

The shoot, including the flowers and fruit, is totally glabrous. Young shoots appear above ground during the summer or fall. The one which I have seen has the distal end turned aside

to a right angle with the erect part, so as to lie parallel with the surface of the earth. When winter is past, this distal end, still in the same position, bears the flowers. Wolf explains that the first part of the shoot to emerge from the ground is not the tip but the middle: the shoot comes up like a bean seedling, as an arch. The arch unbends, but very slowly, so that the end of the shoot may scarcely be fully erect even in fruit. He explains further that the plant is normally sheltered among dead leaves, so as to be found only by raking even when, in fruit, it reaches its greatest height. He regards this shelter as necessary to the life of the plant, which perishes with the forests that furnish it.

My flowering material consists, as I have said, of three shoots. Two of these shoots sprang from opposite sides of a single root: one of them is shown (Pl. 9, fig. 1) the other having been removed. The leaves are spirally arranged obovate obtuse scales attached by the broad base. The details of the arrangement of leaves are inconstant; in order to express what has been seen, it seems expedient to conventionalize, for present purposes, the use of three terms. (a) If we stand above a horizontal root while facing away from its origin, we may designate its sides as right and left as they lie respectively beneath our right and left sides: this convention is the same that is applied to rivers. (b) Following Gray in the choice between the two possibilities, we may designate as a right spiral one which ascends in passing from opposite our left hand to opposite our right hand. (c) By an orthodox spiral, I mean an arrangement of leaves conforming to the familiar $1/2$, $1/3$, $2/5$, etc., system. Now as to the shoots actually seen: of the two which stand upon a single root, the one on the right side shows a right orthodox spiral and the one on the left shows a left orthodox spiral; while the third shoot, alone on its root, shows a left heterodox (approximately $1/4$) spiral. These are mere isolated observations; I do not know that anyone has studied the extent to which the phyllotactic arrangement of leaves is governed by the origin of the shoot which bears them.

Further study of the shoots showing orthodox spirals tended to confirm the doctrine that all orthodox spirals are identical, the apparent different divergences being functions of the extent to which the leaves are crowded. My analysis of the positions of bundles and leaves (Pl. 9, fig. 8) was prepared from the shoot showing a right spiral; as it was prepared with the aid of a compound microscope, the actual directions are reversed, and we have a representation of a left spiral. As we ascend the stem, numbering the leaves beyond any particular one which we designate as leaf zero, we find that leaf 3 falls a certain distance to the left of just above it, and leaf 5 a shorter distance to the right; leaf 8 to the left, but not so far as leaf 3, and leaf 13 to the right, but not so far as leaf 5. A longer stem would doubtless show leaf 21 again to the left and leaf 34 to the right. The actual deviation

is an irrational fraction of a circle which has the property of giving the appearance of an early member of the series, $1/3$ or $2/5$, if the leaves are far apart, and a higher member, $8/21$ or $13/34$, if they are crowded.

Sections of the stem show an epidermis with a longitudinally striate cuticle and an internal mass of parenchyma, of cortex, pericycle, and pith, including many tanniferous cells. Imbedded in the parenchyma is the single cylinder of separate vascular bundles. There is no sheath of fibers. One bundle runs out to each leaf, forking, as it leaves the stem, into three branches. The forking and anastomosis of the bundles which traverse the stem are altogether irregular, a most surprising feature to observe in connection with a perfectly regular arrangement of leaves (Pl. 9, fig. 7, modelled to a definite scale, and fig. 8, representing the internodes as of equal length and the cylinder as unrolled). Within the bundle (Pl. 10, fig. 9), the xylem includes on the side toward the pith a few spiral and annular elements; it consists for the most part of scalariform vessel elements with reticulate cross-walls tilted slightly away from horizontal. There is no cambium; no lateral growth takes place. In the anatomical features mentioned, *Monotropsis* is in good agreement with *Hypopitys* as described by Kamienski (17, 18). This author reported the end-walls of the sieve tubes as devoid of perforations: "Disons franchement que les tubes cribreux ainsi nommés, ne sont pas à proprement parler des tubes, car ils restent fermés par des cloisons transversales, de même qu'ils ne sont pas cribreux car leurs cloisons ne sont pas criblées." He furnished a figure to support this statement. My observations agreed in this point also with his; but I took the precaution of inviting Dr. Katherine Esau to examine my slides. She experienced no difficulty in finding typical sieve plates (Pl. 10, fig. 10); I (and likewise, no doubt, Kamienski) had been deceived by the abundant phloem parenchyma.

THE FLOWER

The inflorescence is a dense raceme of but few flowers. Each pedicel stands in the axil of a bract and bears two bractlets. The flowers are mostly pendant. They are ordinarily pentamerous, but deviations from this condition are common. In my material, one of the terminal flowers is tetramerous, and several flowers, otherwise pentamerous, have a pistil of four carpels. Author after author, beginning with Elliott, has described the flowers as smelling like violets; Wolf describes them as smelling like cloves. The difficulty of describing odors is notorious; undoubtedly, Wolf is referring to the same scent as the other authors.

The sepals (Pl. 10, fig. 11) are separate. The corolla (Pl. 10, fig. 13) is sympetalous, campanulate; at the same time that the petals are laterally united, the base of each one is swollen out into a shallow sac or pocket. One inclines to interpret this sac

as a device for the accumulation of nectar; possibly the nectar is held in place in the inverted flower by capillarity.

There are normally ten stamens. Using purely descriptive language, one may say that the filament is attached to the dorsal side of the anther, within which there is a single chamber opening through two dorsal-distal pores (Pl. 10, fig. 12). Dissection (Pl. 11, figs 16–21) reveals remnants of partitions by which, presumably, the interior of the young anther is divided into four chambers. In the anthers of most angiosperms, that internal wall which lies in a sagittal plane—the connective, separating the two lobes of the anther—is permanent; while in each lobe, the wall in a frontal plane, separating the two microsporangia of the lobe, breaks down before anthesis. In *Monotropsis*, on the other hand, the connective disappears except at the end toward the summit of the flower, between the pores; the frontal walls persist to a slightly greater depth.

I have seen no juvenile anthers. Gray (11) and Wolf account for them as borne in a horizontal position, and Wolf's figures show that the pores originate as slits at the outer ends, where the filaments are attached, each slit crossing the ends of the two microsporangia of one lobe. As the anthers mature, the ends originally inward turn downward (toward the base of the flower) while the pores come to face the summit of the flower. It may be concluded that the outer, apparently dorsal, surface of the mature anther is really ventral; the end toward the base of the flower is the distal end, and the pore-bearing end, facing the summit of the flower, is the proximal end.

The mature pollen grain (Pl. 11, fig. 22) has a thin exine, smooth except for two grooves lying in the same great circle. It contains two dissimilar nuclei. The larger is the generative nucleus; it is spheroidal and is imbedded in a clear space, the generative cell.

Within the bases of the filaments and surrounding the base of the pistil, there is a lobed nectary. Wolf calls attention to Rafinesque's erroneous statement, obviously a mistaken guess, "Stamina 10, a pair between each angle of the nectary." He proceeds to a descriptively correct account of the nectary as five-lobed, the lobes being opposite the petals and emarginate, with one stamen opposite each lobe and one between each pair of lobes. I would place upon the structure a slightly different interpretation: the nectary is ten-lobed; the lobes are in pairs, a pair clasping the base of each petalad stamen.

The pistil is flask-shaped, somewhat shorter than the corolla; the capitate stigma is not evidently lobed. A cross section of the ovary near the base (Pl. 11, fig. 23) shows five (or, often, four) separate chambers. One does not find a single placental mass projected from the axis into each chamber, but two; these are, of course, the margins of the carpels. At any level much above the base of the ovary, a cross section (Pl. 11, fig. 24)

shows the two edges of each carpel completely separate from one another, so that the ovary is unilocular and the placentation parietal. The placentae, throughout the ovary, are densely covered with ovules. The placentae as seen in the upper part of the ovary—each placenta being the fused adjacent edges of two carpels—are continued upward as ridges projecting into the open style channel through which the interior of the ovary is in contact with the atmosphere (Pl. 11, fig. 25).

Sepals, petals, filaments, and the outer surfaces of ovary and style are covered by an epidermis bearing a striate cuticle, enclosing a parenchyma some cells of which are tanniferous, much as in the stems. The anther wall appears to consist of a single layer of collapsed cells. In the neighborhood of the pores there is a distinct tissue evidently involved in dehiscence; its exact nature was not determined, but it appears to be an epidermis of large isodiametric cells which open the pores by contracting hygroscopically.

The vascular supply of each flower originates as one bundle of the cylinder of bundles in the rachis. In this part of the stem, the pericycle is recognizable by a slight differentiation of the cells, not extending to the formation of fibers. Each bundle which passes out to a flower is to be interpreted as a leaf trace completely fused with a branch trace. As it crosses the cortex it gives off a branch to the bract, and as it ascends the pedicel it gives off two branches, one to each bractlet. It enters the receptacle not as a smoothly cylindrical bundle but as a lobed mass which breaks up into four (more or less) main bundles of the flower. These give rise to the following six whorls of bundles in acropetal succession (Pl. 10, fig. 15): (1) a whorl of sepal bundles; (2) a whorl of petal bundles, alternating with the sepal bundles; (3) a whorl of petalad stamen bundles; (4) a whorl of sepalad stamen bundles; (5) a whorl of carpel dorsals, in the planes of the petal bundles; (6) a whorl of placental bundles, in the planes of the sepal bundles. The placental bundles are simply the continuations of the main bundles of the flower. All the bundles of the first five whorls arise either from the dorsal surfaces or from the sides of the main bundles, and leave no gaps; all of them depart at angles greater than 90° , that is, in directions approaching the basipetal. They presently bend and come into the acropetal direction, parallel to the main bundles. In entering the corolla, each petal bundle divides into three branches, of which the median one, the smallest, takes the longest course, following the contour of the sac, while the larger, lateral, bundles ascend past the sac. From the lowest part of the course of the carpel dorsals short obscure branches run out into the nectary. After ascending the walls of the ovary, the carpel dorsals ascend the walls of the style, following the thin strips between the ridges which project into the style channel.

They fade out in the stigma. The placental bundles fade out within the ovary.

The ovary wall is half a dozen cells thick. Its inner epidermis is a layer of elongate, slender cells bearing no cuticle, being indistinguishable except by their shape from the parenchyma of the wall. The epidermis of the placentae consists of rather large, thin-walled, somewhat densely staining cells (one of them is shown in Pl. 11, fig. 28). The inner epidermis of the style is of cells similar to these but elongate, parallel to the axis of the style. Just at the mouth of the style passage, there is some cuticulate epidermis; this cuticle does not extend over the stigmatic surface, being completely separate from the similar cuticle on the outside of the style. The stigmatic surface (Pl. 11, fig. 27) is of large columnar tanniferous cells laterally in contact with one another; their end walls against the atmosphere appear to be thickened but not hardened, as if converted into some gelatinous material.

The ovules are the ordinary ovules of the Monotropeoideae. They are anatropous, with an integument of two layers of cells, of which the outer shows an incipient accumulation of tannin. The nucellus is absent, having been absorbed, when the embryo sac is mature. The embryo sac consists of an egg, two synergids, an endosperm mother cell (in which the two polar nuclei may or may not have fused), and three antipodal cells.

FRUIT AND SEED

When furnishing me with a single fruit, Mr. Spawn explained that he had found very few of them. According to Wolf, few fruits are ever formed: he supposes that the shelter under which the plant lives prevents pollination. The fruit (Pl. 11, fig. 14) remains enclosed in the corolla; it is a berry whose one locule is almost completely filled by the enlarged placentae. The elongate cells of the inner epidermis of the ovary wall, which resemble in shape the similarly placed mechanical cells involved in the dehiscence of the capsules of *Allotropa* and *Pterospora*, become enlarged during the development of the fruit; but, having no mechanical functions, they are not thick-walled and not distinguished by staining reactions. The epidermal cells of the placentae fill much space by becoming elongate at right angles to the surface which bears them. My specimen shows very few seeds; most of the ovules have failed to develop.

PLATE 9. *Monotropis odorata*. Fig. 1. Whole plant $\times 1.6$. Fig. 2. Longitudinal section of root tip $\times 320$. Figs. 3, 4, 5, 6. Cross sections of roots $\times 40$: fig. 3, a small root with diarch xylem; fig. 4, a larger root with pentarch xylem; fig. 5, a root with triarch xylem showing attachment of a secondary root; fig. 6, another section of the same root showing an adventitious bud. Fig. 7. Model of the vascular system through six internodes of stem $\times 8$. Fig. 8. Diagram of the vascular system of the stem through eighteen internodes: the transverse dotted lines represent nodes; the diagonal lines represent the parastichies of the $2/5$ system.

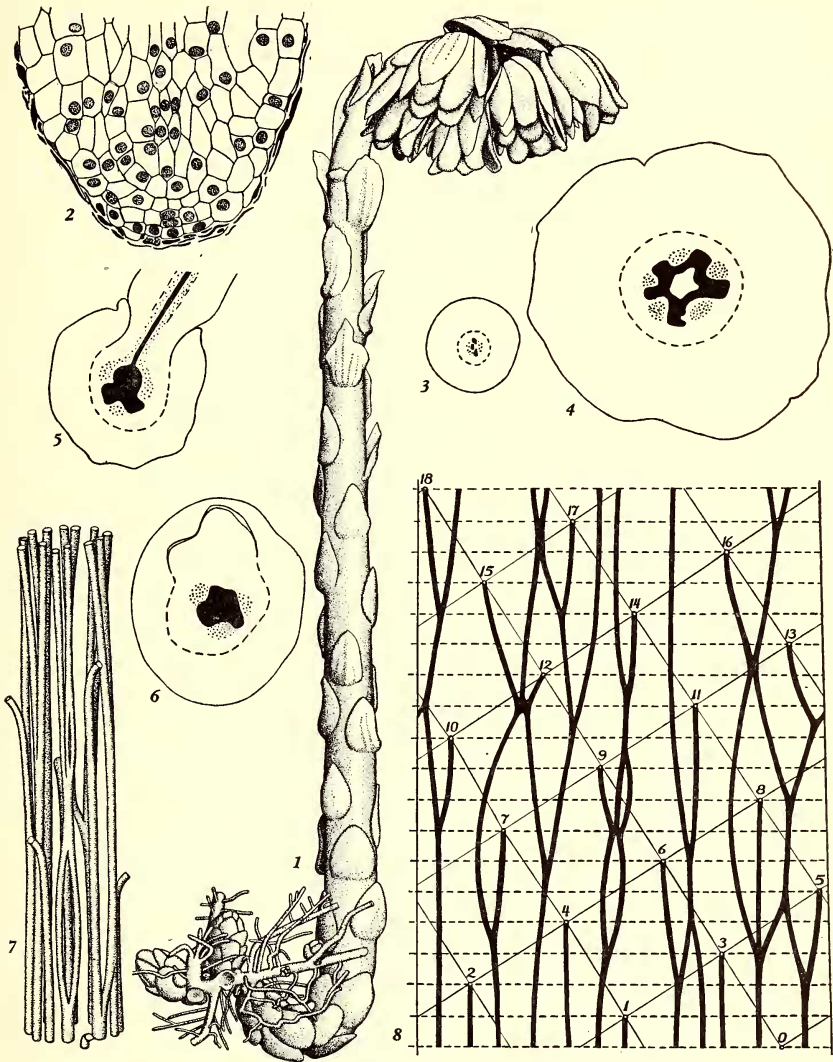


PLATE 9. *MONOTROPSIS ODORATA*.

The seed (Pl. 11, fig. 29) is minute, ovoid, without appendages. The cells of the outer layer of the integument have developed very thick cell walls on their inner and lateral surfaces, while their outer cell walls tend to collapse. The cells of the inner layer of the integument have disappeared except at the ends of the seed. The endosperm is of but few cells and appears to be without haustoria. The embryo is globular; the one most clearly seen appears to consist of just one radially symmetrical tetrad of cells.

RELATIONSHIPS

Among the genera of Monotropeoideae as known to me, the one which is closest to *Monotropis* is *Hypopitys*. Some Monotropeoideae have in the stem a vascular cylinder interrupted only by leaf gaps; these two have a ring of vascular bundles. In the anthers of both, the connective breaks down; in *Hypopitys*, the anther splits from top to bottom (from proximal to distal) in a frontal plane, and becomes explanate. In both genera, the lobes of the nectary are arranged in pairs opposite the saccate bases of the petals. Other genera to be associated with these are the following. (1) *Monotropa* has traditionally included *Hypopitys*. It has separate vascular bundles. The petals are saccate. Pairing of the lobes of the nectary is inconspicuous, but seems to exist. The anthers differ in detail from those of *Monotropis* but agree in essentials. (2) *Pityopus* differs in having in the stem a vascular cylinder interrupted only by leaf gaps, but agrees in having saccate petals, paired nectaries, and anthers like those of *Hypopitys*. (3) *Monotropastrum*, as represented by a specimen of *M. ampullaceum* from Formosa in the Herbarium of the University of California, shows saccate petals and lobes of the nectary not merely approximate in pairs but connate, forming forked structures embracing the bases of the petalad stamens. The idea that the pairing of the lobes of the nectary is worth noticing comes from the paper of Oliver (21). In the genera just listed, I believe that this character is the mark of a derived natural group.

I must withdraw the opinion that *Newberrya* is closer to *Hypopitys* than to *Pleuroscopora*. *Newberrya* and *Pleuroscopora* differ in structure of corolla, in number of placentae, and in pubescence. They agree in having in the stem a vascular cylinder (it is without a sheath of fibers) rather than separate bundles, and in having erect anthers opening through slits. Such anthers are, of course, the ordinary anthers of flowering plants; but here among the Ericales they appear to mark a derived natural group.

PLATE 10. *Monotropis odorata*. Fig. 9. Cross section of vascular bundle $\times 320$. Fig. 10. Longitudinal section of phloem $\times 560$. Fig. 11. Flower $\times 4$. Fig. 12. Flower with perianth removed $\times 4$. Fig. 13. Corolla $\times 4$. Fig. 14. Fruit $\times 4$. Fig. 15. Model of the vascular system in the receptacle of the flower $\times 40$: *Ca*, sepal bundle; *Col*, petal lateral; *Cod*, petal dorsal; *St*, stamen bundle; *Cd*, carpel dorsal; *Pl*, placental bundle.

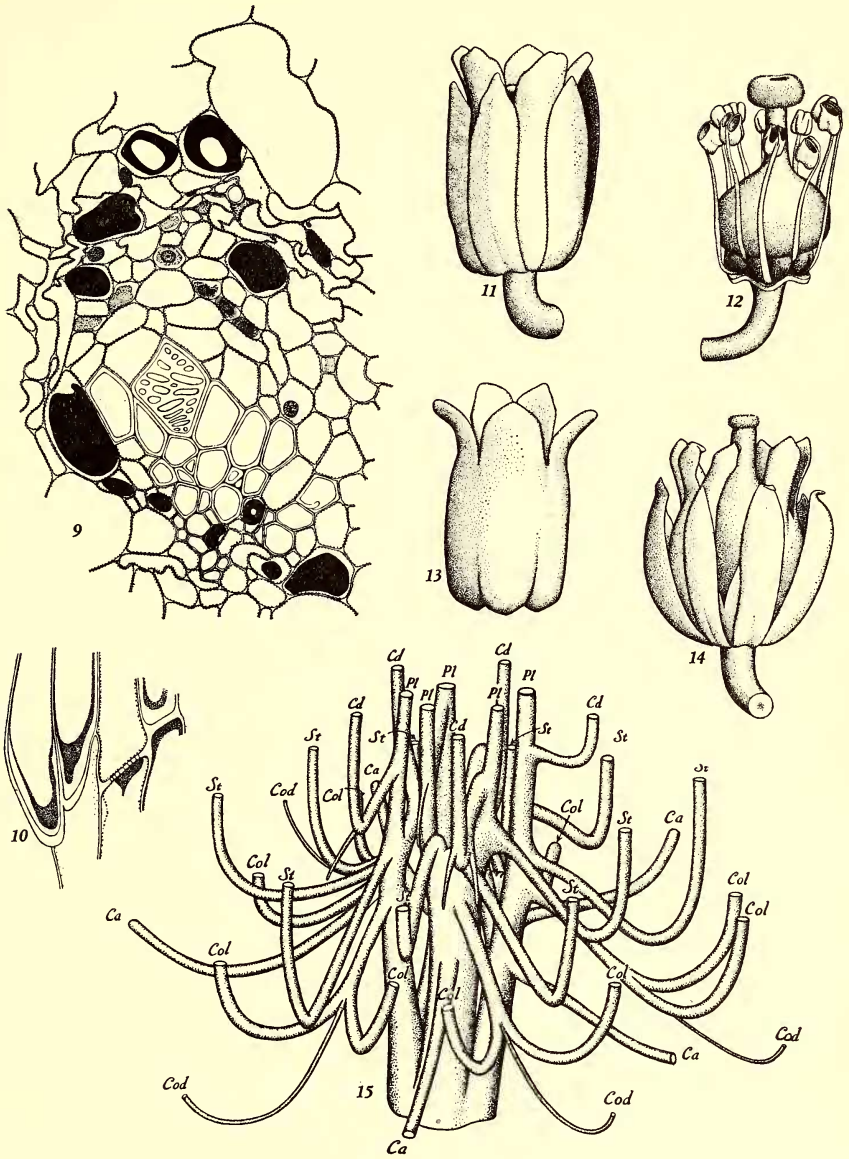


PLATE 10. *MONOTROPSIS ODORATA*.

Of *Cheilothea khasiana* I know little more than the name. It has traditionally been associated with the genera now under discussion. *Wirtgenia* (*Cheilothea malayana* Scortechini ex Hooker f.) has been collected only once, many years ago. The original figure (15) seems to show the evenly placed lobes of the nectary and the erect anthers of the present group; but the alternately long and short stamens remind one of *Monotropas*, next to which Andres has placed it. If we can believe that Hooker misconceived the anthers, this is surely its true position.

The recognition of the groups typified respectively by *Hypopitys* and by *Pleuricospora* leaves us still to place *Sarcodes*, *Pterospora*, and *Allotropas*. Each of these genera exhibits characters unique in Monotropoideae: *Pterospora*, the tailed anthers and seeds with flat wings; *Sarcodes*, the peculiar dehiscence of the fruit; *Allotropas*, asepaly, and anthers which turn upside down during development. The three have in common a stout and erect habit, a vascular cylinder in the stem, surrounded by a sheath of fibers, an ovary with axile placentation in the lower half, and evenly distributed lobes of the nectary. I believe that these characters, as well as the sympetaly seen in *Sarcodes* and *Pterospora*, are the primitive characters of the Monotropoideae. The inversion of anthers during development is shared by *Allotropas* with a strangely scattered list of plants, *Saurauia*, *Clethra*, *Pyrola*, and *Chimaphila*. Formerly I took this also to be a primitive character, but I now suppose that it has appeared independently, at least in the present case: that the original monotropoid plant had anthers pointing inward or downward and opening through pores, as in *Sarcodes*, and bearing tails, as in *Pterospora*. It appears to me that the three genera now under discussion may be recognized as constituting the primitive tribe of Monotropoideae. Their divergences from one another suggest that this is an ancient group. Its geographic limitation to North America, and for the most part to the west coast, may be explained by the assumption that it is of such an age that its distribution is no longer indicative of its place of origin, but has been determined by subsequent history.

It will be seen that I am now content to treat the Monotropoideae as a natural group. My previous uncertainty on this point arose from inability to recognize subordinate natural groups. The difficulty seems to have disappeared upon the assumption that the position of the anthers and the arrangement

PLATE II. *Monotropis odorata*. * Figs. 16, 17, 18, 19, 20. Cross sections of an open anther $\times 20$. Fig. 21. Diagram of a longitudinal section of an open anther $\times 20$, constructed from figs. 16-20, the planes of which are represented by the transverse lines *a* to *e* respectively. Fig. 22. Pollen grain $\times 720$. Figs. 23, 24, 25. Cross sections of a pistil $\times 8$. Fig. 26. Diagram of a longitudinal section of an ovary $\times 8$, constructed from figs. 23-25, the planes of which are represented by the transverse lines *a* to *c* respectively: *plac*, placenta; *Cd*, carpel dorsal bundle; *Pl*, placental bundle. Fig. 27. Radial section through the stigmatic surface $\times 320$. Fig. 28. Longitudinal section of an ovule $\times 320$. Fig. 29. Longitudinal section of the micropylar end of a seed $\times 320$.

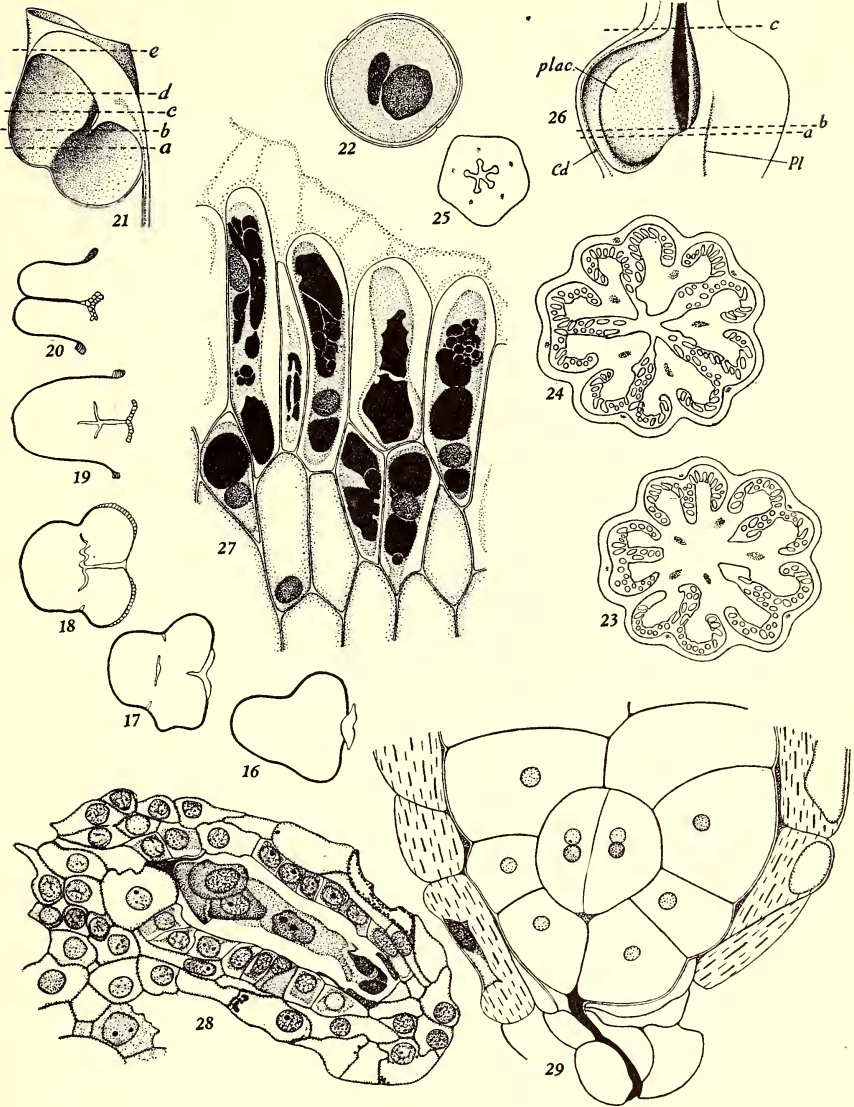


PLATE 11. MONOTROPSIS ODORATA.

of the lobes of the nectary are characters of primary importance. Completely parietal placentation, on the other hand, and likewise choripetalry, seem to have appeared repeatedly. As to the ancestry of the group as a whole, I can support no opinion by much evidence. The problem will no doubt eventually be solved by studies of comparative anatomy; and, considering the tailed anthers of *Pterospora*, I would study first of all the Arbutoideae. The Pyroloideae may well be of the same ultimate origin as the Monotropoideae; but it is not clear to me that these two groups are closer to each other than to any other group of Ericales. We may avoid taking a definite position in a matter which is as yet uncertain by not recognizing the family Pyrolaceae; by including Pyroloideae and Monotropoideae in Ericaceae as separate subfamilies, as in Jepson's treatment (16). The views just stated may be expressed as follows:

ERICACEAE, SUBFAMILY MONOTROPOIDEAE

A. Tip of the filament at maturity bent inward so that the distal end of the anther is directed toward the interior or the base of the flower.

1. Stem including a vascular cylinder with a sheath of fibers; lobes of the nectary evenly spaced; ovary with axile placentation in the proximal part; fruit a capsule:

Tribe PTEROSPOREAE: *Pterospora*, *Sarcodes*, *Allotropia*.

2. Stem including a vascular cylinder or vascular bundles without a sheath of fibers; lobes of the nectary approximate in pairs opposite the saccate bases of the petals; ovary and fruit as above or else unilocular to the base and becoming a berry; anthers at maturity containing a single chamber, sometimes splitting in a frontal plane and becoming explanate:

Tribe MONOTROPEAE: *Monotropsis*, *Hypopitys*, *Pityopus*, *Monotropa*, *Wirtgenia*?, *Monotropastrum*.

B. Tip of the filament erect, the distal end of the anther directed toward the summit of the flower; stem including a vascular cylinder without a sheath of fibers; lobes of the nectary evenly spaced; anthers opening by longitudinal slits; fruit baccate:

Tribe PLEURICOSPOREAE: *Newberrya*, *Pleuricospora*, *Cheilothea*?

Sacramento Junior College,
Sacramento, California, March, 1939.

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OBSERVATIONS ON THE ELONGATION OF THE STIPE OF MONTAGNITES

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Montagnites Candollei var. *texensis* Berk. & Curt. occurs under natural conditions in uncultivated and nonirrigated lands of the University of California Citrus Experiment Station, Riverside, California. The plants are gregarious and appear in March and April after the winter rains if environmental conditions have been favorable. Mature plants are most often found; younger stages are less often seen, probably because of the rapid elongation of the stipe which, under favorable conditions, can carry the spore-bearing part in a few hours from beneath the soil to several inches above it.

Stipe elongation was observed in a young plant in the button stage (text fig. 1, a). At this stage the stipe was the same length